AMMONITES POLYOPSIS DUJARDIN, 1837 AND THE CRETACEOUS AMMONITE FAMILY PLACENTICERATIDAE HYATT, 1900

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ABSTRACT. *Ammonites polyopsis* Dujardin, 1837 is referred to the genus *Placenticeras* Meek, 1876 and shown to have priority over *Ammonites ribourianus* d'Orbigny, 1850, *Placenticeras depressum* Hyatt, 1903, *P. grossouvrei* Hyatt, 1903 (*non* Semenov, 1899) (renamed *P. hyatti* Diener, 1925), *P. incisum* Hyatt, 1903, *P. schlueteri* Hyatt, 1903, and *P. crassatum* Hyatt, 1903 amongst others. This plethora of names results from early failure to recognize the strong dimorphism present in the species. Recognition of this dimorphism and the wide intraspecific variation seen in *P. polyopsis* provides a basis for a review of the Placenticeratidae and its constituent genera, of which revised diagnoses and synonymies are presented. An effect of the nomenclatorial results of the study is that the widely cited. *P. syrtale* Zone should be renamed the *P. polyopsis* Zone.

THE ammonite family Placenticeratidae ranges from the upper Albian to the Maastrichtian. In all probability it was derived from the Hoplitidae via *Hengestites* Casey, 1960 and *Karamaites* Sokolov *in* Casey, 1965. The family is easily recognized by the multiplication of auxiliary and adventive elements in the suture line. At least twenty-four generic names have been established in the family, and a large number of specific names, yet the wide range of variability within taxa has been known for more than 150 years. Placenticeratids have a sporadic occurrence in western Europe but are sufficiently widespread and frequent in the upper Santonian and Campanian to be used as zonal indices in the standard scheme erected by de Grossouvre (1901). Although Hyatt (1903) renamed many of the European *Ammonites syrtalis* of Schlüter (1871-6) and *Placenticeras syrtale* of de Grossouvre (1894) only two years after the *syrtale* Zone was introduced, and made it quite plain that true *P. syrtale* (a North American lower Campanian species) did not occur in Europe, the *syrtale* Zone has persisted in the literature, including the *Lexique Stratigraphique International* (e.g. Sornay 1957) and recent syntheses (e.g. Wright 1957; Basse 1960; Collignon 1960; Pessagno 1969; Séronie-Vivien 1972; Rawson *et al.* 1978; van Hinte 1979; Wiedmann 1979; Hancock and Kennedy 1981). Summesberger (1979) has used the name *Stantonoceras depressum* (Hyatt, 1903) for this European form, but has recognized dimorphism.

We describe below the material from Touraine, Aquitaine, and the Corbières in France on which de Grossouvre (1901) based the *syrtale* Zone, and show that the correct name for the species is *P. polyopsis* (Dujardin, 1837), of which *S. depressum* is a synonym. The range of intraspecific variation in *P. polyopsis* and the marked dimorphism present provides a basis for a survey of all the generic taxa proposed in the family, their diagnoses and synonymies.

SYSTEMATIC PALAEONTOLOGY

Location of specimens. This is indicated by the following abbreviations: BM(NH), British Museum (Natural History), London; IGS, Institute of Geological Sciences, London; MNHP, Muséum National d'Histoire Naturelle, Paris; SP, Collections of the Sorbonne, now housed in the Université de Paris VI; FSR, Faculté des Sciences, Rennes; EMP, École des Mines, Paris Collections, now housed in the Université Claude-Bernard, Lyon; FSM, Faculté des Sciences, Le Mans, which now houses the collections of the Musée de Tessé, Le Mans.

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Dimensions. Dimensions are given in millimetres, in the following order: diameter (D), whorl breadth (Wb), whorl height (Wh), and breadth of umbilicus (U); c = costal; ic = intercostal. Figures in parentheses refer to dimensions as a percentage of diameter.

Suture terminology. The suture terminology of Wedekind (1916; see Kullman and Wiedmann 1970) is followed here; I = Internal lobe, U = Umbilical lobe, L = Lateral lobe, E = External lobe.

Family PLACENTICERATIDAE Hyatt, 1900
Genus *Placenticeras* Meek, 1876

Placenticeras polyopsis (Dujardin, 1837)

Plates 86–88; text-figs. 1–4

1837 *Ammonites polyopsis* Dujardin, p. 232, pl. 17, fig. 12.
1850 *Ammonites polyopsis* Dujardin; d'Orbigny, p. 212.
1850 *Ammonites Ribourianus* d'Orbigny, p. 213.
1872 *Ammonites syrtalis* Morton; Schlüter, p. 46, pl. 14, figs. 1–10; pl. 15, fig. 5, *non* figs. 1, 2 (= copy of Morton 1834), 3–4 (= *Proplacenticeras pseudorbignyanum* (Hyatt, 1903)).
non 1872 *Ammonites polyopsis* Duj. (?); Fritsch, p. 35, pl. 6, fig. 3.
1883 *Ammonites Ribourianus* d'Orbigny; Arnaud, pl. 3.
non 1893 *Ammonites polyopsis* Duj.; Fritsch, p. 76, text-fig. 56.
1894 *Placenticeras syrtale* Morton; de Grossouvre (*non* Morton), p. 128 (*pars*), pl. 5, fig. 3; pl. 6, figs. 1, 2; pl. 7, fig. 1; pl. 8, fig. 1 (including var. *quadratum*).
non 1895 *Placenticeras polyopsis* Dujardin; Jahn, p. 130.
1903 *Placenticeras depressum* Hyatt, p. 237.
1903 *Placenticeras grossouvrei* Hyatt, p. 237.
1903 *Placenticeras incisum* Hyatt, p. 238.
1903 *Placenticeras schluteri* Hyatt, p. 239.
1903 *Placenticeras polyopsis* (Dujardin); Hyatt, p. 240.
1903 *Placenticeras crassatum* Hyatt, p. 241.
1916 *Placenticeras syrtale* Mort. var. *guadaloupe* F. Roemer; Stolley, p. 93, pl. 5, fig. 4.
1925 *Placenticeras crassatum* Hyatt; Diener, p. 185.
1925 *Placenticeras depressum* Hyatt; Diener, p. 185.
1925 *Placenticeras Hyatti* Diener, p. 185.
1925 *Placenticeras incisum* Hyatt; Diener, p. 185.
1925 *Placenticeras polyopsis* Dujardin; Diener, p. 188.
1925 *Placenticeras Schlüteri* Hyatt; Diener, p. 189.
1931 *Placenticeras syrtale* Mort. var. *guadaloupae* F. Röm.; Riedel, p. 695.
?1931 *Placenticeras syrtale* Mort. cf. var. *milleri* V. Hauer; Riedel, p. 696.
?1931 *Placenticeras syrtale* Mort. var. *costata* Riedel, p. 696, pl. 79, fig. 2.
1937 *Placenticeras* cf. *guadalupae* F. Roem.; Riedel, p. 217, pl. 16, fig. 3.
?1937 *Placenticeras radiatum* (J. Böhm in sched.); Riedel, p. 219, pl. 16, figs. 1, 2.
1963 *Placenticeras* cf. *hyatti* Diener; Fabre-Taxy, p. 108, pl. 3, fig. 3.
?1963 *Placenticeras orbignyanus* Geinitz sp.; Fabre-Taxy, p. 109.
1963 *Stantonoceras guadaloupae* Roemer sp.; Fabre-Taxy, p. 109, pl. 3, figs. 5–7.
1963 *Stantonoceras* cf. *ribouri* d'Orbigny; Fabre-Taxy, p. 110, pl. 3, figs. 8, 9.
1963 *Stantonoceras sancarlosense* Hyatt sp. var. *collignoni* nov. var.; Fabre-Taxy, p. 111, pl. 3, figs. 12, 13.
?1963 *Stantonoceras* sp.; Fabre-Taxy, p. 111.
1978 *Stantonoceras depressum* (Hyatt); Wiedmann, p. 667, pl. 1, figs. 1, 2; text-figs. 2B, 3A.
1979 *Stantonoceras depressum* Hyatt; Summesberger, p. 145, pl. 10, figs. 42, 43; pl. 11, figs. 44–47; pl. 12, figs. 48–52; text-figs. 31–37.

Types. Dujardin based this species on two specimens (1837, pl. 17, fig. 12*a* and *b–c*; see text-fig. 1). The original of his fig. 12*a*, a juvenile macroconch, is here designated lectotype. Both specimens are said to be from the 'Craie Tufau', and no locality, other than Touraine, is given. They have not been traced.

Material. From St.-Patern-Racan, variously labelled 'route' or 'niveau à *Spondylus truncatus*': FSR, three specimens (plus one unlabelled that is probably from this locality); MNHP B16692; FSM, one unregistered

specimen (*ex* Guiller Coll.). MNHP B16802 from the Craie de Villedieu of Loir-et-Cher. MNHP B16802 from Couture, Villedieu-le-Château. Several specimens (Gale Coll.) from Bed 22a (Jarvis *et al.* 1982) of the Craie de Villedieu at La Ribochère, Loir-et-Cher. MNHP unregistered from near Villandry, Indre-et-Loire. MNHP unregistered from Savonnières (Indre-et-Loire). BM(NH) C26681 and an unregistered specimen in the EMP collections (*ex* Deshayes Coll.), both from Tours. EMP unregistered (*ex* Thomas Collection) from Langeais, Indre-et-Loire.

There are numerous specimens from Aquitaine. The Arnaud Collection, now in the Sorbonne Collections housed in the Université de Paris VI, includes the best localized specimens from Arnaud's assize M^2 at Miremont, Riberac, Périgueux, Beaulieu (Siolac, souterrain de Beaulieu); from M^{1-2} at Angoumac, Cognac; from M^2 at Champagnac-de-Belair, St. Léon-sur-Vezère, Versannes, Epagnac, Miremont, Puygaty, and Rognac; one specimen is precisely located as from couche 22, route d'Agonac, Périgueux. From N^{1-2}, a specimen of *P.* cf. *polyopsis* from St. Caprais; from N^2 at Arcivaux, Saintes, a *P.* cf. *polyopsis*. All but one of the specimens figured by de Grossouvre (1894) have not been traced (they are probably in the Université de Paris VI but are not available; a set of casts is in the collections at Rennes and those of the École des Mines, now at Lyons); they are from M^2 at Beaulieu, and La Valette. A specimen in the EMP collections (*ex* Boucheron Collection) is also from the last locality. A further specimen in the Collections of the Musée de Gaillac is from Charmant.

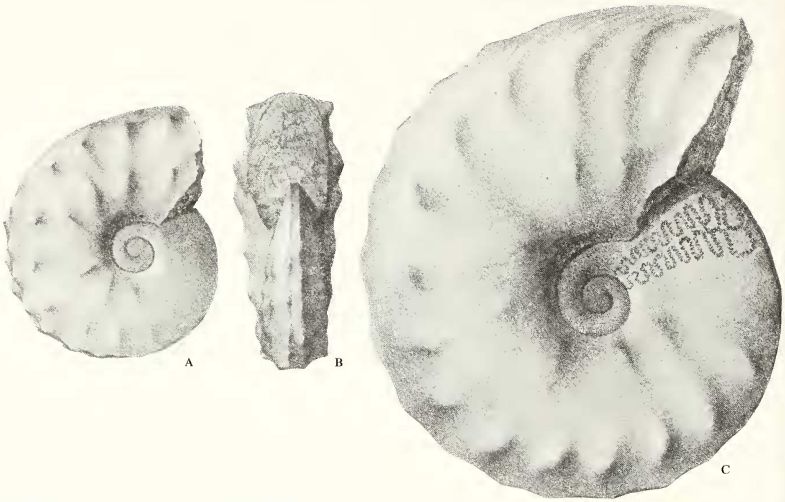
There are numerous specimens from the Corbières (Aude), variously labelled Sougraines, environs de Rennes-les-Bains, Chemin de Croutets, etc., in the MNHP, SP, EMP, FSL, and BM(NH) collections. Stratigraphic data are usually poor, but de Grossouvre (1901, p. 795) notes that it is rare in the lower part of the Santonian but common in the upper part.

Dimensions		D	Wb	Wh	Wb:Wh	U
Microconchs:						
MNHP B16692	c	72·0 (100)	28·7 (39·9)	30·7 (42·6)	0·94	19·6 (27·2)
	ic		23·4 (32·5)	30·7 (42·6)	0·76	
FSR L803		79·7 (100)	— (—)	39·8 (49·9)	—	16·5 (20·7)
MNHP 'Villandry'	c	109·5 (100)	— (—)	46·3 (42·3)	—	26·2 (23·9)
	ic	133·0 (100)	41·4 (31·1)	55·4 (41·7)	0·75	31·5 (23·7)
MNHP unreg. at	c	109·0 (100)	41·0 (37·6)	50·0(45·9)	0·82	23·5 (21·6)
	ic	109·0 (100)	34·0 (31·2)	47·0 (43·1)	0·72	
Macroconchs:						
MNHP 'Savonnièrs'		106·5 (100)	— (—)	55·0 (51·6)	—	20·5 (19·2)
MNHP 16802		141·0 (100)	— (—)	64·0 (45·4)	—	30·0 (21·3)

Description. The species is strongly dimorphic, as demonstrated by Summesberger (1979).

Microconchs. The inner whorls up to a diameter of 30–40 mm are compressed, involute, with a small crater-shaped umbilicus (around 15% of the diameter) (Pl. 87, fig. 4). The umbilical wall is flattened and slopes outwards; the umbilical shoulder is abruptly rounded. The whorl section is compressed (whorl breadth to height ratio 0·6 or less), with the greatest breadth close to the umbilical shoulder, the inner flanks rounded, the outer flanks converging to a narrow tabulate venter with sharp ventrolateral shoulders. There are feeble comma-shaped umbilical bullae (six per half whorl in MNHP B16691) which give rise to low, broad prorsiradiate ribs that flex back and are feebly concave, that is falcoid, on the outer flank, and appear to terminate in feeble ventral clavi (the specimens are defective on this point). From around 40 mm the whorls change from compressed with a narrow venter to trapezoidal with a broad, flattened venter and eventually become depressed on the adult body chamber with the greatest breadth at strong umbilicolateral bullae and below mid-flank intercostally. The feeble bullae of the inner whorls strengthen markedly, and migrate out from the umbilical shoulder to first an inner (Pl. 86, fig. 2), and ultimately a mid-flank position (Pl. 87, fig. 6). A low broad rib connects them to the umbilical seam of a large, moderately deep umbilicus, the wall of which merges imperceptibly with the flank. These tubercles are rounded to bullate, strong on the phragmocone and early body chamber of adults, but decline towards the adult aperture to weak, sharp bullae only (Pl. 85, fig. 2).

The umbilicolateral tubercles give rise to one or a pair of low, broad, straight, prorsiradiate ribs and there are also occasional short intercalated ribs to give a total of nine per half whorl. All ribs bear rounded-clavate inner ventrolateral tubercles that strengthen progressively around the outer whorl. Corresponding to each of these is a



TEXT-FIG. 1. *Ammonites polyopsis* Dujardin, 1837 (pl. 17, figs. 12*a–c*). Copy of Dujardin's original figures. A, B, paralectotype. C, lectotype.

sharp elongate ventrolateral clavus. This initially sits on the sharp ventrolateral shoulder of a rather narrow venter but, as size increases and the venter broadens, the clavus becomes progressively weaker and is eventually reduced to the merest swelling on a blunt angulation between a broad venter and broadly rounded ventrolateral shoulder. The clavi and ribs on opposite flanks vary from slightly offset to alternate in position. The venter is crossed by broadly convex growth lines and striae. The largest observed microconch (Pl. 85, figs. 1–3) has an estimated diameter of 120 mm with just over half a whorl of body chamber, the coiling becoming progressively more evolute towards the aperture.

Macroconchs. The ornament and shell form of nuclei is identical to that of the microconchs described above. The compressed, relatively feebly ornamented or smooth stage persists, however, to a diameter of 60–70 mm (Pl. 86, fig. 4); thereafter an ornament of falcoid ribs with feeble inner and stronger outer ventrolateral clavi is succeeded by an adult whorl which remains compressed but develops initially weak and bullate but subsequently strong and conical umbilicolateral tubercles which migrate to first a mid- and then an outer-flank position. These tubercles are linked to the umbilical shoulder by a low, weak rib, and give rise to a pair of low, broad, straight ribs, each of which bears a clavate inner ventrolateral tubercle. These are initially set at an angle to the line of the venter, but rotate to parallel the venter as size increases. These tubercles are invariably weaker than those of microconchs at the same diameter. Outer ventrolateral clavi are borne on the ventrolateral shoulder, generally offset from or alternating with those on the opposite side of the narrow venter. They persist to the largest diameter seen, a phragmocone 150 mm in diameter (text-fig. 2).

The suture line (text-fig. 3) follows the sagging course typical of the genus. Development of adventive and auxiliary elements gives an adult suture with eight bifid saddles in the external part.

Discussion. This species is surrounded by nomenclatorial confusion because most authors failed to recognize that individuals of the same size with markedly different ornament were dimorphs. The name *Ammonites polyopsis* was validly introduced by Dujardin in 1837, and accompanied by excellent illustrations, reproduced here as text-fig. 1.

In his description (1837, p. 232), Dujardin comments: 'Cette ammonite varie tellement, que des échantillons isolés pourraient être pris pour des espèces distinctes, si l'on n'observait quelquefois toutes les variations possibles sur les différents points d'un même échantillon.'

The lectotype (Dujardin 1837, pl. 17, fig. 12*a*; see text-fig. 1C) is a juvenile macroconch, and the paralectotype (Dujardin 1837, pl. 17, fig. 12*b–c*; see text-fig. 1A, B) is a microconch. D'Orbigny listed *A. polyopsis* in the *Prodrome* (1850, p. 212, no. 15), and indicated that there were specimens in his collection. The catalogue records two specimens under no. 7180, from Tours (Indre-et-Loir). One of these specimens survives, and is a fragment of a mature microconch. D'Orbigny also introduced the name *A. semiornatus* in the *Prodrome* (1850, p. 212). The remarks are characteristically brief: '*13. *semiornatus*, d'Orb., 1847. Espèce tres-aplatie; à tours embrassants, lisses, tronqués sur la carène, et ornés de chaque côté de cette partie de tubercles obliques. Tours, route de Paris.' This is a perfectly valid indication and two specimens survive in d'Orbigny's collection, under no. 7179. Sornay (1955) has refigured the material, referring it to *Diplacmoceras* (*recte Diplacomoceras*) and designating the complete specimen lectotype. Its horizon is unknown, but probably Santonian; a specimen from the Craie de Villedieu of St. Frimbault, Sarthe (MNHP de Vibraye Collection, 1896. 27) in a preservation identical to that of *Protexanites bourgeoisi* (d'Orbigny, 1850) from this locality is of upper Coniacian date. It differs from *Placenticeras polyopsis* in lacking umbilical tubercles at any stage, and in having low, rursiradiate concave ribs on the outer flank of the early stages that migrate outwards and turn into rounded or bullate inner ventrolateral tubercles that are associated with twice their number of ventral clavi. On the lectotype these rotate progressively around the body chamber to lie parallel with the venter.

A second name introduced by d'Orbigny in 1850 (p. 213) was *A. ribourianus*: '*49. *Ribourianus*, d'Orb., 1847. Espèce voisine de l'*A. polyopsis*, mais avec le dos carré, et deux rangées latérales de tubercles aigus. France, Villedieu (Loir-et-Cher), M. Bourgeois.' The asterisk indicates that d'Orbigny had specimens in his collection, but none is listed in the catalogue. From the description it clearly represents the microconch of *P. polyopsis*, body chambers of which indeed have a square back and two rows of pointed lateral tubercles.

Schlüter (1872, p. 46) treated *A. polyopsis* as a junior synonym of *A. syrtalis* Morton, 1834 (p. 40, pl. 16, fig. 4), a view followed by de Grossouvre (1894, p. 128). Both these authors recognized the wide variation in morphology and ontogeny shown by the species, and also placed *A. geinitzii* d'Orbigny, 1850 (p. 213, = *A. vibrayeanus* Geinitz (*non* d'Orbigny), 1843, p. 8, pl. 1, fig. 8), *A. guadaloupae* Roemer, 1852 (p. 32, pl. 2, fig. 1), and *A. milleri* Hauer, 1866 (p. 5, pl. 2, figs. 1, 2) in synonymy.

A. syrtalis Morton, 1834, is a lower Campanian species and was revised by Hyatt (1903), Reeside (1927), and Young (1963) while Wolleben (1967) has provided a valuable analysis of populations of this species. Even Hyatt (1903, p. 196) realized the wide variation of the species: 'There is no real line between *P. guadalupae*, *sancarlosense* and *planum*, nor between *newberryi* and *guadalupae*, nor between *sancarlosense*, *syrtale*, *intercalare* and *placenta*, nor between *intercalare*, *stantoni*, *pseudoplacenta* and *whitfieldi*.' Wolleben (1967) placed all these species in synonymy, as well as *Stantonoceras pseudocostatum* Johnson, 1903 and *P. rotundatum* Johnson, 1903. He recognized, however, a series of chronological subspecies: *P. syrtale syrtale* (oldest), in which specimens of '*P. syrtale*' of previous authors are abundant, *P. syrtale adkinsi* Wolleben, 1967, in which specimens of '*P. pseudosyratale*' of previous authors are abundant, and *P. syrtale rooneyi* Wolleben, 1967, in which specimens of '*P. newberryi*' of previous authors are abundant. Nomenclatorial problems of this treatment aside, it was unfortunate that Wolleben failed to recognize that this species shows the same type of dimorphism as *P. polyopsis*, with robust '*Stantonoceras*' microconchs and '*Placenticeras*' macroconchs.

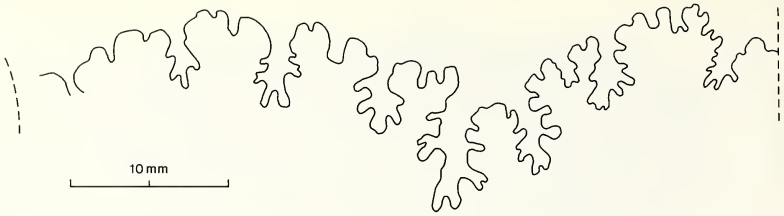
P. syrtale is superficially similar to *P. polyopsis*, but Hyatt (1903) recognized them as separate, noting that juveniles of the American species lack ribs on the inner whorls and that umbilical bullae remain on the umbilical shoulder, not showing the outwards migration of the French specimens. The sutures are also different, *P. polyopsis* having eight lobes in the external suture and *P. syrtale* ten or eleven.

TEXT-FIG. 2. Immature macroconch of *Placenticeras polyopsis* (Dujardin, 1837), MNHP B16802, from 'Loir-et-Cher', ×1.

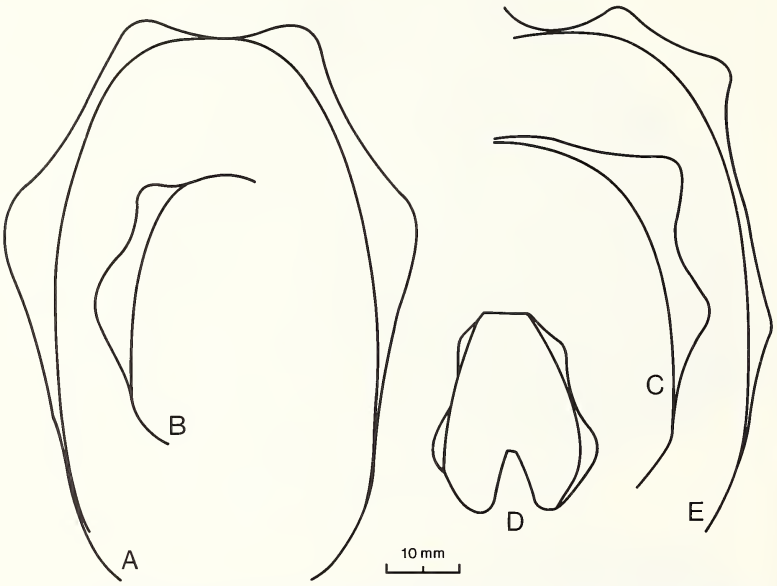
EXPLANATION OF PLATE 85

Figs. 1–3. *Placenticeras polyopsis* (Dujardin, 1837). Slender microconch from the Santonian Craie de Villedieu of Touraine (MNHP unregistered, *ex* de Grossouvre Collection). ×1.

KENNEDY and WRIGHT, *Placenticeras*



TEXT-FIG. 3. External suture of *Placenticeras polyopsis* (Dujardin, 1837), based on an unregistered specimen in the Sorbonne Collections (ex Toucas Collection), from near Sougraines, Corbières, Aude.



TEXT-FIG. 4. Whorl sections of *Placenticeras polyopsis* (Dujardin, 1837). A, slender microconch (see Pl. 86, figs. 1–3 for details). B, C, microconch from Couture, MNHP B16805; B is at the beginning of the body chamber, C at the end. D, phragmocone of an immature microconch from near Villandry, MNHP collections. E, phragmocome of macroconch shown in text-fig. 2.

EXPLANATION OF PLATE 86

Figs. 1–5. *Placenticeras polyopsis* (Dujardin, 1837). 1–3, MNHP B16692, immature microconch from the Santonian Craie de Villedieu of St.-Paterne-Racan, Indre-et-Loire. 4, 5, MNHP B17228, immature macroconch from the Santonian of Paulin, Dordogne. All × 1.

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2

3

4

5

KENNEDY and WRIGHT, *Placenticeras*

Hyatt (1903) renamed most of Schlüter's (1872) and de Grossouvre's (1894) *A. syrtalis* and *P. syrtale*. *P. depressum* Hyatt, 1903 (p. 237) (= *A. syrtalis* Schlüter (*non* Morton), 1872, p. 46 (*pars*), pl. 14, figs. 9, 10 only; *P. syrtale* var. *Guadaloupae* de Grossouvre (*non* Roemer) 1894, p. 128, pl. 6, fig. 2 only; pl. 7, fig. 1, lectotype here designated, the original of de Grossouvre 1894, pl. 6, fig. 2) is a microconch *P. polyopsis*. *P. hyatti* Diener, 1925 *nom. nov. pro P. grossouvrei* Hyatt, 1903 (p. 237) (*non* Semenov, 1899) = '*Placenticeras syrtale* de Grossouvre (*pars*), p. 128, pl. 5, fig. 32, p. 16, fig. 1 (no others)' was cited erroneously in Hyatt's posthumous work, 'pl. 5, fig. 32, p. 16, fig. 1' not existing in de Grossouvre's work. From the subsequent account, however, it is apparent that the intended citation was 'pl. 5, fig. 3, pl. 6, fig. 1'. The latter is here designated lectotype of the species; it is an adult macroconch. The paralectotype is a juvenile 55 mm in diameter that already has ribs and tubercles at the smallest diameter visible, indicating it to be a juvenile microconch.

P. incisum Hyatt, 1903 (p. 238) (= *P. syrtale* de Grossouvre, 1894, p. 128 (*pars*), pl. 8, fig. 1 only) is based on a macroconch from assize M^2 of Arnaud at La Valette (Charente) (Rejaudry Collection). It has not been traced (but there are casts in the FSR and EMP collections) and a fine unlocalized specimen in the MNHP collections, illustrated here as Pl. 85, figs. 1–3, serves as a basis for discussion. The dimensions are given above. Ornament consists of umbilicolateral tubercles, of which there are seven on the outer whorl. These are weak and markedly bullate at the smallest diameter visible, but strengthen markedly and migrate outwards around the last whorl and are connected to the umbilical seam by a low rib. Very weak pairs of ribs link to strong inner ventrolateral clavi, whilst additional clavi are intercalated to give a total of approximately twenty per whorl. Those on opposing flanks are slightly offset in ventral view, rising high above the narrow venter. At the smallest diameter visible a semicontinuous ridge or angulation marks the junction of venter and ventrolateral shoulder, but this declines on the body chamber where the venter is smooth and concave between persistent ventral clavi. This early decline of outer ventrolateral clavi, and the angulation marking their site which disappears on the body chamber, are features of microconch *P. polyopsis*, but these are generally depressed and quadrate. At the same diameter, similarly compressed macroconchs are still septate and retain discrete outer and inner ventrolateral clavi. The species is interpreted as an unusually compressed microconch of *P. polyopsis*.

P. schluteri Hyatt, 1903 (p. 239) (= *A. syrtalis* Schlüter (*non* Morton), 1872, p. 46 (*pars*), pl. 14, figs. 1, 2) was separated by Hyatt on the basis of details of ornament and ontogenetic changes in tuberculation. The specimen shows the same outward migration of umbilicolateral tubercles as *P. polyopsis* but lacks ribs on the inner flank; it is a clear synonym, and probably a microconch. *P. crassatum* Hyatt, 1903 (p. 241) (= *A. syrtalis* Schlüter (*non* Morton), 1872, p. 46 (*pars*), pl. 14, figs. 4–7, fig. 3?) was differentiated from *P. schluteri* by Hyatt because it was more compressed and did not show an outward migration of the umbilicolateral tubercles which disappear and are replaced by low ribs. This is probably no more than a variant of *P. polyopsis*.

P. pseudorbignyanum Hyatt, 1903 (p. 242) (= *A. syrtalis* Schlüter (*non* Morton), 1872, p. 46 (*pars*), pl. 15, figs. 3–5 only) is a member of the Coniacian *P. orbignyanum* (Geinitz, 1850) group which lacks the strong tubercles of the later *P. syrtale*. Other members are *P. fritschii* de Grossouvre, 1894 (p. 124, pl. 5, figs. 1, 2; text-fig. 52) (the type species of *Proplacenticeras* Spath, 1926), *P. memoriaschloenbachi* (Laube and Bruder, 1887) (p. 221, pl. 23, fig. 1), *P. kaffrarium* (Etheridge, 1904) (p. 89, pl. 3, fig. 16), *P. umkwelanensis* (Etheridge, 1904) (p. 89, pl. 3, figs. 17–20), and *P. subkaffrarium* (Spath, 1921)

EXPLANATION OF PLATE 87

Figs. 1–6. *Placenticeras polyopsis* (Dujardin, 1837). 1, 2, SP unregistered, juvenile microconch from the Souterrain de Beaulieu on the line from Ribérac to Périgueux, Dordogne; figured by de Grossouvre (1894, pl. 5, fig. 3). 3, 4, MNHP B16691, incomplete microconch showing smooth inner whorls, from the Santonian Craie de Villedieu of Monnat, near Villandry, Indre-et-Loire. 5, 6, MNHP unregistered, incomplete microconch from the Santonian Craie de Villedieu, 2 km west of Villandry, Indre-et-Loire. All × 1.

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(p. 247, pl. 21, fig. 2). These show a wide range of intraspecific variation and dimorphism comparable in some respects to that seen in *P. polyopsis*, as will be discussed in a forthcoming publication.

P. syrtale costata Reidel, 1931 (p. 696, pl. 79, fig. 2) from the Santonian of Ziegeli near Recklinghausen in the Münster Basin is regarded as no more than a variant of the present form, as is *P. radiatum* Riedel, 1937 (p. 219, pl. 16, figs. 1, 2) from the Santonian of Heudeber-Danstedt in the Harz Foreland. However, more and better material of both forms might in future indicate consistent differences justifying subspecific separation.

P. paraplanum Wiedmann, 1978 (p. 666, pl. 1, figs. 3, 4, text-fig. 2A; see also Summesberger 1979, p. 152, pl. 13, figs. 53–57, text-figs. 38, 39) which occurs with *P. polyopsis* in the upper Santonian Gosau Beds of Gosau, Austria. It appears to be separate from *P. polyopsis* on the basis of strongly convex flexuous ribs and bullae that remain closer to the umbilical shoulder. Wiedmann compared it to *P. planum* Hyatt, 1903, which Wolleben (1967) considered no more than a variant of *P. syrtale*, and it may lie in an analogous position in the spectrum of variation of *P. polyopsis*. One of the specimens referred to the species by Summesberger (1979, pl. 13, figs. 55, 56) shows an outward migration of the umbilicolateral bulla and an early decline of the outer ventrolateral clavi.

P. maherndli Summesberger, 1979 (p. 155, pl. 14, figs. 58–61; pl. 15, figs. 62–66, text-figs. 40–47) is a much better characterized species in which Summesberger was also able to recognize dimorphism. It occurs with *P. polyopsis* in the upper Santonian Gosau Beds of Gosau, Austria. Inner whorls bear falcoid ribs, the macroconch develops weak bullae, and body chambers of both forms bear dense flexuous ribs. Distinct as this appears, the material is no more different from the *P. polyopsis* described here than the extremes of *P. syrtale* discussed by Wolleben (1967) are from each other.

Occurrence. The species is confined to the Santonian. In Touraine it occurs widely in the Craie de Villedieu, well-localized specimens coming from de Grossouvre's (1901) Zone E, the niveau à *Spondylus truncatus* of previous authors. Jarvis *et al.* (1982) have shown that the species occurs in the remanié lag at the top of a hardground (their bed 22a) at Villedieu; the preservation of other specimens suggests a similar occurrence. The only associated fauna of stratigraphic significance is *Baculites incurvatus* Dujardin, 1837. In Aquitaine the species is widespread, as indicated under the list of specimens studied, and Arnaud (1877) cited it from many other localities (see also Séronie-Vivien 1972). The stratigraphic range spans all of Arnaud's divisions of the Santonian (M^1, M^2, N^1, N^2), and this is confirmed by records in Toucas (1883), de Grossouvre (1894, 1901), and Séronie-Vivien (1972). The last author recorded it from only 5 m above the base of the Santonian in a temporary trench at L'Amblardie, Montmoreau (p. 78), and low in the Santonian at Castelfadèze and Mater (pp. 89, 144). Indeed, most of Arnaud's specimens are from his divisions M^1 and M^2—that is to say, the lower Santonian *Texanites texanus* Zone of de Grossouvre.

In the Corbières the reliable records are still those of de Grossouvre (1894, 1901), who recorded it as rare in the lower part of the sequence (his *texanus* Zone) but common above (the 'banc à *Lima marticensis*' and the 'marnes intercalées entre les deux principaux bancs de rudistes'). This is what Bilotte *et al.* (1971) referred to as the 'Série de la Montagne des Cormes'. The species occurs at many localities in the Beausset Basin (Var) (de Grossouvre 1894, 1901; Fabre-Taxy 1963). Fabre-Taxy assumed all the occurrences to be in the upper Santonian.

In Austria the species is abundant in the Gosau and Piesting areas (Wiedmann 1978; Summesberger 1979, 1980). The Gosau records are in the 20 m thick 'sandkalkband' at the top of the Santonian. This species occurs widely in the Germanies, and Mr. C. J. Wood has kindly analysed the best-documented occurrences. At Deitermann's brick-pit at Rapen, near Recklinghausen, the Recklinghausen Marl yielded *P. polyopsis* associated with *Boehmoceras krekeleri* (Wegner, 1905) and *B. loescheri* (Riedel, 1931) and other species. These suggest the upper Santonian on the basis of Summesberger's records and the occurrence of *Boehmoceras* in Arnaud's Assizes M^2 and N^2 in Aquitaine. The Recklinghausen occurrences are associated with *Marsupites*, indicating the *M. testudinarius* Zone of the north-west European White Chalk facies. Böhm (1915) recorded *P. schlueteri* Hyatt, 1903 (e.g. *P. polyopsis*) associated with *B. krekeleri* and other ammonites in the *M. testudinarius* Zone at Ahaus. Riedel (1937) recorded what are here interpreted as *P. polyopsis* from the Salzberg Marl of the Quedlinburg–Salzberg region; the associated inoceramid evidence indicates the high *Micraster coranguinum* Zone of the White Chalk facies. He recorded from Heudeber–Danstedt what he believed to be different species, *P. radiatum* and *P. intercalare*, herein regarded as *P. polyopsis*, associated with a fauna indicating a higher horizon than that at Salzberg.

The more general records of Wiedmann (1979) appear to be based chiefly on Schlüter's early records; they

suggest *P. polyopsis* is confined to the upper part of the Santonian; indeed, Wiedmann uses the term *syrtale* Zone in de Grossouvre's sense.

These data suggest that *P. polyopsis* ranges from just above the base of the Santonian in Aquitaine to the highest of Arnaud's divisions (from M^1 to N^2). Most of the surviving specimens are labelled M^1, but there are so few that this may not reflect real abundance. In the Corbières the species occurs both low and high in the Santonian but is commonest above. The same appears to be true in Provence and in Germany and Austria. The Touraine records are stratigraphically isolated and cannot be referred to either upper or lower Santonian with any confidence at this time. The absence of diagnostic elements of the high Santonian crinoid zones of the White Chalk facies (Jarvis *et al.* 1982) suggest it is lower Santonian, however, as that term is used in the chalk sequences.

Dr. W. A. Cobban (pers. comm., 1982) tells us that he believes fragments of *Placenticeras* from the Tombigbee Sand Member of the Eutaw Formation of Alabama can be referred to the present species; the unit is assigned to the Santonian on other evidence.

DISCUSSION

Stratigraphic consequences. The upper Santonian *P. syrtale* Zone of de Grossouvre and authors should be renamed the *P. polyopsis* Zone. The index species, however, has a range that extends into the lower Santonian.

Systematic consequences. The recognition of wide intraspecific variation and dimorphism in *P. polyopsis* leads to a critical review of the systematics of the Placenticeratidae.

The family appears to have evolved rapidly in the upper Albian from *Metaclavites* Casey, 1965 (Hoplitinae) by increase in whorl height and associated development of extra elements in the suture. Almost all members of the family up to the Maastrichtian show at some stage of ontogeny the alternating ventrolateral clavi that characterize their hoplitine ancestors.

In the upper Albian there are three genera whose interrelationships are not yet clear. *Hengestites* Casey, 1960, known only from England, has a juvenile stage with feeble flexuous ribs ending in fine ventrolateral clavi. The shell then becomes smooth with sharp-edged, sulcate, later tabulate, venter; the suture is not far removed from that of Hoplitinae but shows major subdivision of saddle E/L. *Hypengonoceras* Spath, 1922, known from Spain, Madagascar, Zululand, southern India, and perhaps Japan, has low falcoid ribs and ventrolateral clavi to a late stage, together with a suture characterized by many subequal pincer-like saddles. The third genus, for which *Karamaites* Sokolov in Casey (1965, p. 461) is the earliest of seven names which we regard as synonymous, ranges from upper Albian to Cenomanian and is known from France, Crimea, and Central Asia. It has flat sides on the early whorls which become convex later, and ventrolateral tubercles which persist to a variable extent. The suture is also variable but the 4th lateral lobe is generally smaller than the 5th.

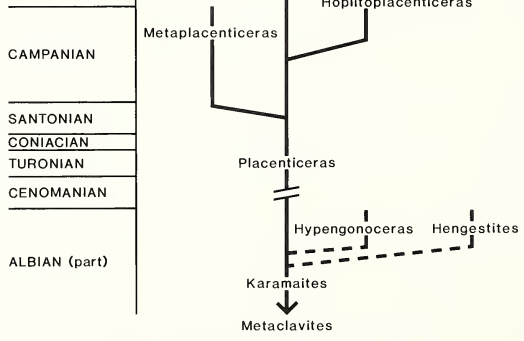
Karamaites begins the mainstream of the family which continues with slow elaboration of ornament and suture until the Maastrichtian. Marked dimorphism can be demonstrated whenever large collections of upper Cretaceous specimens are examined. We have insufficient Albian material to pronounce on dimorphism, but in the upper Cenomanian *Proplacenticeras* from Texas it is obviously present, the macro- and microconchs differing in size, but little else. By the upper Turonian the Madagascan faunas show an association of large forms that are said to be smooth when adult, except for minute umbilical tubercles (*Proplacenticeras memoriaschloenbachi* var. *ambiloensis* Collignon, 1965*a*, p. 14, pl. 381, fig. 1646; pl. 382, figs. 1647–8), and smaller forms with stronger umbilical bullae and weaker clavate mid-lateral to inner ventrolateral and outer ventrolateral tubercles (*Parastantonoceras murphyi* Collignon, 1965*a*, p. 17, pl. 382, fig. 1649); these we take to be macro- and microconchs respectively. The same type of dimorphism may also be present in the so-called 'Middle' Turonian of Madagascar (see Collignon 1965*a*, pl. 383), with '*Parastantonoceras*' *besairiei* (Collignon, 1936) as microconch, and in the Coniacian with *Proplacenticeras fritschi eboroensis* Collignon, 1965*b* (p. 38, pl. 430, figs. 1780–1781) as macroconch and *P. kaffrarium* (Etheridge, 1904) as microconch (the nomenclature of Coniacian '*Proplacenticeras*' is as confused as that of the Santonian species of *Placenticeras* and is not entered into here).

The dimorphism shown by the European *Placenticeras polyopsis* is described above. Suture line apart, macroconch *Placenticeras* and '*Proplacenticeras*' are very similar, differing only in the degree

of retention of strong ornament and outward migration of umbilical bullae and mid-lateral clavi. The microconchs become more evolute and are sometimes quadrate in whorl section, with persistent ornament. The same is true of the Campanian *Placenticeras syrtale* group, as documented, but not recognized, by Wolleben (1967).

Two stocks separated from *Placenticeras* in the Santonian that in our view clearly deserve generic separation. *Metaplacenticeras* Spath, 1926, is characterized by dense strong flexuous ribbing and no tubercles. We have not seen enough material to recognize dimorphism. *Hoplitoplacenticeras* Paulcke, 1906, is relatively evolute with a more or less rectangular whorl section and strong ribs and tubercles and lacks a smooth stage. Preliminary observations on material from Zululand (South Africa) indicate dimorphism.

Given the wide range of variation of ornament and progressive increase in numbers of sutural elements, it is difficult to decide on any split in generic classification of the mainstream forms. It would be attractive to refer the whole of the mainstream of the family to one genus, *Placenticeras*, with *Karamaites*, *Proplacenticeras*, and *Placenticeras sensu stricto* as successive subgenera for those who can find significance in minor sutural differences. It is in our view practicable in the present state of knowledge to distinguish *Karamaites*, generically or subgenerically, for early forms in which definite dimorphism is not yet demonstrated. *Proplacenticeras*, however, is tied to its type species, *Placenticeras fritschi* Grossouvre, and study of the type material shows that it is either conspecific with or very closely allied to contemporary material from Zululand (Klinger and Kennedy 1980, p. 305) that covers a morphological range almost as wide as that of Santonian *Placenticeras*. The progressive increase in the number of auxiliary elements in the suture does not, we believe, allow any sensible division; if reliance were placed on this character a distinct genus or subgenus would logically have to be based on each increase of one new auxiliary lobe in the adult suture. The outward migration in strongly ornamented forms of umbilical tubercles to a mid-lateral position and of mid-lateral tubercles to an inner ventrolateral position is equally continuous. Our conclusion is that we should for the present at least maintain *Karamaites* for mainstream forms that show no strong differentiation of dimorphs and group in *Placenticeras* those upper Cenomanian, Turonian, and later species, including the type species of *Proplacenticeras*, that have strongly differentiated microconchs. If *Karamaites* is subsequently found to have strongly differentiated microconchs, it should be reduced to a synonym of *Placenticeras*. We would thus set out the classification of the family as follows (see also text-fig. 5):



TEXT-FIG. 5. Phylogeny of the Placenticeratidae.

Family PLACENTICERATIDAE Hyatt, 1900, p. 585
(= Hypengonoceratidae Chiplonkar and Ghare, 1976, p. 2; Baghiceratinae Chiplonkar and Ghare, 1976, p. 3)

Diagnosis. Moderate-sized to large; inner whorls at least generally involute, compressed, with narrow flat or grooved venter and little or no ornament; outer whorls similar in macroconchs; microconchs of some genera become evolute and more or less inflated with strong ornament. Suture with adventive and auxiliary elements; the external saddle and first lateral lobe become very wide and develop a number of more or less equal new elements; saddles and lobes may be short and more or less rounded, or long, narrow-necked, and much frilled. Of Albian genera, while *Hypengonoceras* in some respects resembles Engonoceratidae, *Hengestites* and *Karamaites* are clearly derived from Hoplitidae.

Occurrence. Upper Albian to Maastrichtian.

Genus *Hengestites* Casey, 1960, p. 201

Type species. *Hengestites applanatus* Casey, 1960, p. 201, by original designation.

Diagnosis. Large, high-whorled, involute with angular umbilical rim and narrow venter. Early whorls have faint flexuous riblets ending in alternating ventrolateral clavi. Later shell is smooth, the venter sulcate with carinate edges, then tabulate. Suture with shallow ventral lobe, a broad bifid or asymmetrically trifid first lateral lobe, bifid and subphylloid saddles; a deep adventitious lobe divides the external saddle unequally, the ventral part being much smaller.

Occurrence. Upper Albian; England.

Genus *Hypengonoceras* Spath, 1922, p. 112

Type species. *Placenticeras warthi* Kossmat, 1895, p. 92, by original designation.

Diagnosis. With sloping flat sides and narrow flat venter; sparse low falcoid ribs end in alternating ventrolateral clavi. Suture with large pincer-like bifid folioles.

Occurrence. Upper Albian; Spain, Madagascar, Southern India, ?Japan.

Genus *Karamaites* Sokolov *in* Casey, 1965, p. 461

Synonyms. *Karamaites* Sokolov, 1961, p. 152 (*nom. nud.*); *Karamaiceras* Sokolov, 1967, p. 138; *Turkmenites* Ilyin, 1975, p. 154; *Kopetdagites* Ilyin, 1975, p. 157; *Mediasiceras* Ilyin, 1975, p. 159; *Beschtubites* Ilyin, 1975, p. 162.

Type species. *Placenticeras grossouvrei* Semenov, 1899, p. 97, by original designation.

Diagnosis. Sides flat at first, then inflated and convex; weak sinuous to falcoid ribs may be present on early whorls, with little ornament except for prominent alternate ventrolateral clavi which persist to body chamber. Suture with 4th lateral lobe generally smaller than 5th. So far as is known, dimorphs are not strongly differentiated.

Occurrence. Upper Albian to Cenomanian; France, Central Asia.

Genus *Placenticeras* Meek, 1876, p. 462

Synonyms. *Placentocerus* Meek, 1871, p. 429, *nom. oblit.*; *Diplacomoceras* Hyatt, 1900, p. 585; *Diplacomoceras* Hyatt, 1903, p. 242; *Stantonoceras* Johnson, 1903, p. 208; *Proplacenticeras* Spath, 1926, p. 79; *Pseudoplacenticeras* Spath, 1926, p. 79; *Anaplacenticeras* Ilyin, 1959*a*, p. 201; *Gissarites* Ilyin, 1959*b*, p. 727; *Parastantonoceras* Collignon, 1965*a*, p. 17; *Asiatostantonoceras* Ilyin, 1975, p. 172; *Baghiceras* Chiplonkar and Ghare, 1976, p. 3; *Malwiceras* Chiplonkar and Ghare, 1976, p. 4; *Placentoscaphites* Chiplonkar and Ghare, 1977, p. 68; *Sancarlosia* Chiplonkar and Ghare, 1978, p. 79.

Type species. *Ammonites placenta* DeKay, 1828, p. 278, by subsequent designation by Meek, 1876, p. 462.

Diagnosis. Distinguished from *Karamaites* by progressive increase in number of elements in the suture line, by development of strongly differentiated microconchs, and by progressive outward migration of umbilical tubercles to mid-lateral and mid-lateral to inner ventrolateral positions. Extreme forms are smooth, involute discs with narrow tabulate venters on the one hand and on the other forms with evolute, square-sectioned outer whorls with strong ribs and lateral and ventrolateral tubercles.

Occurrence. Upper Cenomanian to Maastrichtian; world-wide.

Genus *Metaplacenticeras* Spath, 1926, p. 79

Synonym. *Paraplacenticeras* Matsumoto, 1953, p. 149.

Type species. *Placenticeras pacificum* J. P. Smith, 1900, p. 187, by original designation of Spath, 1926, p. 79.

Diagnosis. Compressed and flat-sided; with rather strong falcoid or falcate ribs; venter distinctly tricarinate, at least in middle growth. Line of suture follows that of ribs.

Occurrence. ?Santonian, Campanian; Japan, California.

Genus *Hoplitoplacenticeras* Paulcke, 1906, p. 183 (ICZN name no. 1348)

Synonym. *Dechenoceras* Kayser, 1924, p. 175.

Type species. *Hoplites-Placenticeras plasticus* Paulcke, 1906, p. 186: ICZN Opinion 554, 1959: name no. 1629.

Diagnosis. Rather evolute, whorl section compressed or trapezoidal, venter flat; with prominent variable coarse rounded or dense fine ribs, nearly straight, with inner and outer ventrolateral tubercles, of which outer may be large and clavate; ribs cross venter transversely and may have trace of siphonal tubercle.

Occurrence. Campanian–Maastrichtian; France, Germany, West Africa, Egypt, Zululand (South Africa), India, British Columbia, Texas, Wyoming, Patagonia.

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